Reproductive biology of the unstriped grass rat, *Arvicanthis,* in East Africa

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Abstract

A total of 749 *Arvicanthis* was collected from two areas in western Uganda and a third area in central Kenya to compare breeding biology and life history strategies in different environments.

Breeding was continuous in western Uganda, but in central Kenya, where the environment was more seasonal, breeding ceased towards the end of the dry season. No relationship was observed between the breeding season and diet. Factors accounting for the breeding rhythm in different environments are discussed.

Breeding rates, litter size, and potential production rates tended to increase as the environment became more variable, and body size and age of first reproduction tended to decrease. The trends were generally consistent with the theory of r- and K-selection.

Introduction

The unstriped grass rat or Nile rat is common in savanna and cereal cropland in the Nile valley and much of Africa south of the Sahara and north of the Zambezi (KINGDON 1974). It is an important agricultural pest (TAYLOR and GREEN 1976) and a carrier of various diseases including bubonic plaque (HEISCH et al. 1953; MISONNE 1959; DAVIS 1963).

It is a highly plastic genus with regard to coat colour, size, and minor variations of skull and tooth form. Consequently the status of many of the described forms is uncertain. MISONNE (1971) only recognized one species, *niloticus* (Desmarest), but suggested that some of the pale-bellied forms might be a distinct species. In East Africa two species have been recognized: a dark-bellied form, *niloticus*, and a white-bellied form called *lacernatus* Rüppel by KINGDON (1974) and *testicularis* (Sundevall) by DELANY (1975). However, ROSEVEAR (1969) in a very careful comparison of West African forms concluded that belly colour was an unreliable criterion and grouped *testicularis* with *niloticus*. Chromosome studies have revealed that there are at least two species in this genus because the form *niloticus* has a karyotype of 56 chromosomes (MATTHEY 1965), and *abyssinicus* Rüppell a karyotype of 62 chromosomes (MATTHEY 1959). The genus is obviously in need of taxonomic revision.

The breeding biology of *Arvicanthis* also appears to be variable (DELANY and NEAL 1969; TAYLOR and GREEN 1976; MÜLLER 1977). This paper documents the breeding biology of two populations from western Uganda and a third population from central Kenya. The breeding biology of these populations is compared to populations from western Kenya (TAYLOR and GREEN 1976) and Ethiopia (MÜLLER 1977) firstly to shed some light on the environmental factors responsible for the initiation of breeding, and secondly to discuss the life history and in particular, reproductive strategy, of this genus.

Study areas and climate

The two areas in western Uganda were located in the Ruwenzori (formerly Queen Elizabeth) National Park. Most animals were trapped at Mweya Peninsula (0° 11' S, 29° 54' E) within an area of approximately 1 km², at an altitude of 950 m. The area was mainly within 100 m of housing where the grassland was considerably modified by repeated cutting. The dominant grass was *Cynodon dactylon*, and *Panicum maximum, Sporobolus pyramidalis, Chloris gayana, C. pycnothrix*, and *Cenchrus ciliaris* were also abundant. Animals were also collected from the Crater Track region (0° 06' S, 29° 54' E) 10–13 km north of Mweya Peninsula, within an area of approximately 8 km², at an altitude of 1000–1100 m. The vegetation was dense grassland, 90–120 cm high, dominated by *Imperata cylindrica, Themeda triandra*, and *Cymbopogon afronardus*. A more detailed description of the area is provided by NEAL (1970).

Rainfall and temperature were monitored at Mweya Peninsula. Rain is expected throughout the year but the pattern is seasonal. There are normally two rainy seasons, during the periods March until May and September until November (McCALLUM and HANNA 1969). The June to July dry season is normally more severe than the January until February dry season. There was little seasonal variation in temperature, the mean monthly temperature ranged from 22.9 to 23.9 °C during the period of study.

Animals were collected from five localities in Meru National Park in central Kenya. Almost all of the animals were collected from the southern edge of the Rojewero Plains (0° 11' N, 38° 10' E) within an area of approximately 2 km², at an altitude of 650 m. The plains are open grassland dominated by *Chrysopogon plumulosus, Sehima nervosum, Cenchrus ciliaris*, and *Chloris virgata* (AMENT 1975). There were a few stunted trees, mainly *Combretum apiculatum, Acacia* sp. and *Terminalia* sp. *Arvicanthis* were almost exclusively trapped under and around fallen trees. A few animals were collected from four other areas within a 10 km radius of the Rojewero Plains. They were all similar to the Rojewero population, with the exception of those collected from the Mururi Swamp, 6–7 km northwest of the Rojewero Plains.

Rainfall and temperature were monitored at the Park headquarters, 3 km east of the main trapping area. There are normally two rainy seasons, during the periods March until May and October to December (MORTH 1970). The probability of rain during the dry seasons is low, so that rainfall is more seasonal than in western Uganda. The seasonal variation in temperature was also greater than in western Uganda, the mean temperature ranging from 25.2 °C to 29.9 °C during the period of study.

Materials and methods

A total of 438 *Arvicanthis* was trapped at Mweya Peninsula, 87 from the Crater Track region, 224 from the Rojewero Plains, and 3 from the Mururi Swamp. The areas were sampled by standard trap lines spaced approximately 50 m apart with the traps at 10 pace intervals. Collections were made monthly for a period of at least a year in the three main study areas. Animals were measured, weighed and sexed soon after removal from the traps. A clean body weight was obtained by removing the gut, from the lower oesophagus to the rectum, and also the uterus and embryos of pregnant females.

The female reproduction tract was examined before and after fixation in Bouin's solution and animals categorized as immature if they had a thin, non-vascularized uterus, and no placental scars or corpora lutea were observed. Mature females were categorized as 1. visibly pregnant (i. e. with implanted embryos); 2. reproductively active if visibly pregnant, or the uterus was distended and well vascularized, or corpora lutea were observed; and 3. reproductively inactive if the uterus was thin and poorly vascularized and no corpora lutea were visible. The ovaries of animals collected in Kenya were also serially sectioned. Five animals were reclassified after examination of the sectioned ovaries. All were females which were initially categorized as immature but which were found to have corpora lutea and were, therefore, reclassified as reproductively active mature animals. Thus, the classification based on the gross morphology of the reproductive tract was generally reliable.

The male reproductive organs were dissected out and weighed after preservation in Bouin's solution. A sperm smear was taken from each cauda epididymidis. Individuals were classified as 1. immature if no sperm was visible; 2. sub-adult if only a few sperm were present among fat globules; and 3. adult if sperm were abundant. It was assumed that only adult males were fecund.

The relative age of individuals was estimated using the eruption and subsequent wear of the upper molars as a criterion (NEAL 1968). Seventeen preliminary age-classes were identified based on the way in which the dentine of individual cusps joined as a result of tooth wear. The preliminary age-classes were grouped to give 12 final age-classes.

Stomachs of the Kenya animals were preserved in Bouin's solution and after transfer to 70 % alcohol were examined microscopically using a polarized light system. The identification of plant and

animal material was facilitated by their different birefringence patterns, but quantification of different plant types was not attempted because the food particles were generally very small and diverse. Replicate slides were made and the relative surface area of plant and animal material assessed visually until their percentage could be determined with a standard error of less than five percent. This normally involved the measurement of 100–200 food particles. A note was also made if seeds were common.

The potential annual production of young per female, P, was estimated for each locality using the equation:

$$P = \overset{\text{season}}{\Sigma} \ (L \cdot T/I)$$

where L is the litter size in the wet or dry seasons, T is the length of the wet and dry seasons, and I is the interval between litters in the wet and dry seasons. It is possible to estimate or measure L and T directly and I was estimated for each season using the following equation:

$$I = p_o + p_I + p_v$$

where p_o is the mean length of the non-pregnant period, p_I is the length of the preimplantation period when embryos are not macroscopically visible, and p_v is the length of the gestation period when embryos are macroscopically visible. Obviously the gestation period is the sum of p_I and p_v. The value of p_v was estimated to be about 14 d, because the gestation period is about 18 d (Davis 1963) and p_I is approximately 4 d because the implantation sites in most small rodents become macroscopically visible on the fifth day of gestation (Snel and Stevens 1966; Layne 1968). The combined value of p_o and p_I was estimated for each season by the following equation, which is a modification of the equation given by Butynski (1979):

$$Nv/(N_o + N_I) = p_v/(p_o + p_I)$$

where N_v is the number of females with implanted embryos, and $(N_o + N_I)$ are the number of adult females without implanted embryos. This method overestimates the actual annual production of young per female because it ignors the mortality of adult females.

Results

Body characteristics

The various populations of *Arvicanthis* differed markedly in their body weights and weights of the adult male reproductive organs (Table 1). The two Ugandan populations were only 10–13 km apart, and the two Kenyan populations only 6–7 km apart, and yet there was no overlap in the size and weight of the adult testes and the two Kenyan

Table 1

Body weights and weights of male reproductive organs of various populations of *Arvicanthis* (g)

| | Uganda | | Kenya | | |
	Mweya Peninsula	Crater Track	Rojewero Plains	Mururi Swamp	Other Studies
Birth weight	2½–3	2½–3	3–3½	–	4–6[1]
Weanling weight	15–25	15–25	15–20	–	
Weight at puberty ♀	55–65	c. 60	20–35	–	c. 45[2]
♂	65–80	c. 60	33–40	–	
Adult weight ♀ (range)	60–110	60–90	35–70	80–89	140–150
(mean)	86 ± 1.4	74 ± 1.8	49 ± 1.4		66[2a]; 84[2b] c. 95[3]
Adult weight ♂ (range)	70–125	60–90	35–65	91	140–175[1]
(mean)	98 ± 1.3	75 ± 2.1	52 ± 1.2		89[2a]; 98[2b] c. 95[3]
Weight adult testes	1.1–2.2	0.28–0.51	0.08–0.23	0.5	
Weight adult seminal vesicles	0.1–1.2	0.05–0.31	0.03–0.3	0.14	

[1] Laboratory population from Dakar, Senegal (Quilici et al. 1969). – [2] Field population at Kitale, W. Kenya (Taylor and Green 1976); [2a] no wheat supplement; [2b] fed wheat supplement. – [3] Field population in Semien Mountains National Park, Ethiopia (Müller 1977)

populations also differed markedly in their adult body weights. These results suggest that these populations are reproductively isolated from one another and there are strong selection pressures maintaining these differences.

It has been noted that animals from wetter areas tend to be larger than those from drier areas in both West Africa (ROSEVEAR 1969) and East Africa (KINGDON 1974). My data (Table 1) are consistent with this observation, but animals collected from western Kenya (TAYLOR and GREEN 1976) and Ethiopia (MÜLLER 1977), where the annual rainfall is considerably heavier than western Uganda, were no larger or even not as heavy as the Mweya Peninsula population (Table 1). However, the climate in these wetter areas was more seasonal than that recorded in western Uganda, and this in part may explain the discrepancy.

Adult males were a little heavier than adult females at Mweya Peninsula, western Kenya, and in a laboratory population from Senegal (Table 1). There was no evidence of sexual dimorphism in other populations although males tended to mature at a heavier body weight than females on the Rojewero Plains.

Breeding season

Reproductively active males and gravid females were collected throughout the year at Mweya Peninsula, and reproductive activity appeared to be at a maximum during the rains (Fig. 1 A, B, D). Only 35 adult females were collected from the nearby Crater Track area. Reproductively active females were present every month (except August when no adult females were collected) and pregnancies were recorded during the periods March to July and September to December. Thus, the general pattern of breeding appeared to be similar in the two localities in western Uganda.

Reproductively active males and females were also collected throughout the year on the Rojewero Plains, but breeding ceased towards the end of the dry season when the mean temperature was at a maximum (Fig. 2 A, B, D). The lack of conceptions in October and March to early April, which had small samples, was confirmed by the absence of any females with recent placental scars in the November and April samples.

The difference in breeding seasons in western Uganda and central Kenya was expected because rainfall was more seasonal in Kenya (Figs. 1 D, 2 D). The speed of the breeding response to increased rainfall was also different in the two areas. Immature males and adult females in western Uganda began to mature or increase their reproductive activity the month after the increased rainfall in August 1965, and breeding peaked in October, two to three months after the start of the rains (Fig. 1A, B, D). There was little synchrony in conceptions and females were collected at all stages of gestation in September and October 1965. In contrast, the breeding response to increased rainfall was extremely rapid in central Kenya (Fig. 2 B, D) and, as a consequence, the conceptions were more synchronized. There was an obvious progression in the breeding data collected at the end of the dry season and beginning of the rains (Table 2). Most conceptions occurred one to two weeks after the onset of the rains, although a few individuals conceived during the first week of the rains.

The pattern of breeding in central Kenya was very similar to that reported for the Northern Sudan (HAPPOLD 1975), except that there is only one rainy season in July to September at Khartoum. However, in agricultural areas around Kitale in western Kenya, where there is normally a single rainy season from March until September (MORTH 1970), *Arvicanthis* ceased breeding around the middle of the dry season and did not begin again until two to three months after the start of the rains (TAYLOR and GREEN 1976). However, they bred almost continuously if cereals were artificially supplied. WATSON (1950) suggested a possible breeding season towards the end of the rains in eastern Uganda because
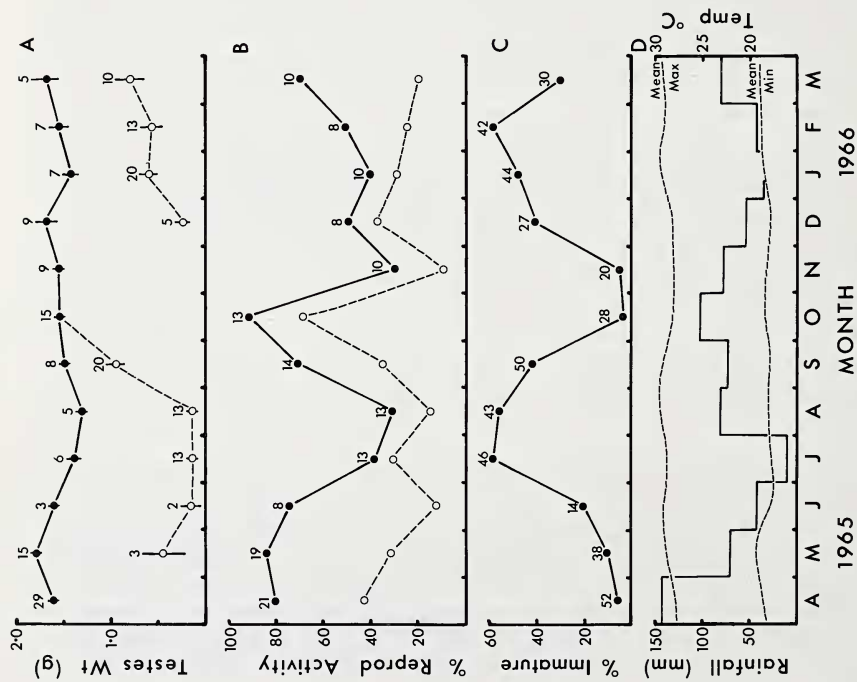
Fig. 1. Seasonal changes in reproductive activity of *Arvicanthis* at Mweya Peninsula, in relation to monthly rainfall and temperature. Numbers in figures A–C indicate sample sizes. A: ——— adult males, ---○--- immature or maturing males; B: ——●—— overall adult female reproductive activity (see text), ---○--- visibly pregnant
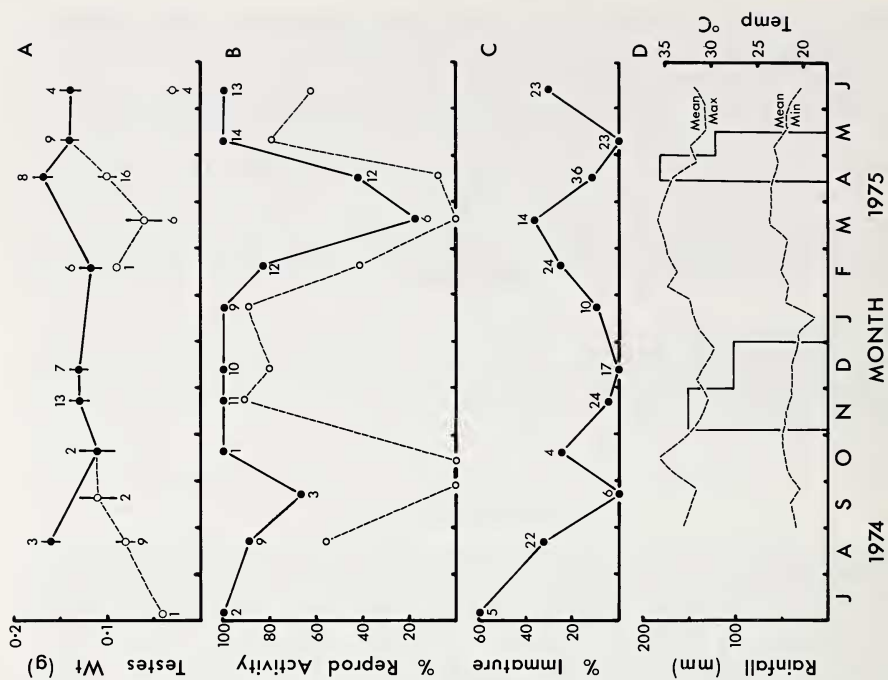
Fig. 2. Seasonal changes in reproductive activity of *Arvicanthis* at Rojewero Plains in relation to rainfall and temperature. Notation as in Fig. 1

Table 2

Reproductive condition and stage of gestation of adult females collected at the end of the dry season and beginning of the rains in the Meru National Park, Kenya

Time in relation to start of rains	No. of adult females			Length of Embryos mm
	Corpora lutea absent	Corpora lutea present Not visibly pregnant	Visibly pregnant	
2–23 d before rains (Oct., March, April data)	7	2	0	–
Rains start + 3–5 d (April data)	5	1	0	
+ 6–8 d (April data)	0	3	1	< 1
+ 13–17 d (Nov. data)	0	0	3 2	< 1 5½–7
+ 18–21 d (Nov. data)	0	1	3 2	< 1 7–10
+ 27–32 d (May data)	0	3[1]	1 3 2 5	8–9½ 10–15 16–19 20–28

[1] parous females

Arvicanthis were very numerous during the early part of the dry season. Finally, in the Ethiopian highlands breeding was confined to the dry season (MÜLLER 1977), possibly because of the cold, damp conditions that exist during the rains. It is obvious that the pattern of breeding in relation to rainfall is very variable in this genus.

Breeding rates

There was no significant difference in breeding rates between the two localities studied in Uganda, and so the results have been combined for the following comparison of breeding rates. The pattern of breeding in Uganda (Fig. 1) and Kenya (Fig. 2) was best predicted by the pattern of rainfall accumulated over a two month period. This seems biologically reasonable because it incorporates a time lag including the effects of rainfall as well as current rainfall conditions. On this basis the dry periods were defined as those months in which less than 100 mm of rain had accumulated over a two month period (July–August and January–February in western Uganda, and July–October and February–early April in central Kenya), and the wet periods included the other months of the year.

Female reproductive activity and pregnancy rates were compared (Table 3) and found to be significantly higher during the wet seasons, although the level of significance was only 10 % in the case of pregnancies in Uganda. The inverse relationship between breeding activity and percentage of immatures was consistent with this seasonal breeding pattern (Figs. 1 B, C; 2 B, C). Reproductive activity and pregnancy rates were significantly higher in central Kenya compared to western Uganda (Table 3), except for pregnancy rates during the dry seasons. Thus, there was a greater amplitude in seasonal breeding rates in Kenya compared to Uganda, which was expected because rainfall was more seasonal.

In western Kenya the pregnancy rate was approximately 50 % in the main breeding period during the rains (TAYLOR and GREEN 1976), compared to rates of 38 % and 69 % observed during the rains in western Uganda and central Kenya (Table 3). Approximately 24 % of the adult females were pregnant during the dry season in Ethiopia (MÜLLER 1977),

Table 3

Comparison of adult female reproductive activity and pregnancy rates in wet and dry seasons and different localities

Proportions tested for independence by chi-squared analysis of 2 × 2 contingency tables (SOKAL and ROHLF 1969)

Locality	Wet season	Dry season	Comparison of seasons
	Proportion reproductively active		
Uganda	95/133	21/49	$\chi^2 = 12.7$***
Kenya	62/67	24/35	$\chi^2 = 10.0$***
Comparison of localities	$\chi^2 = 11.8$***	$\chi^2 = 5.4$**	
	Proportion visibly pregnant		
Uganda	50/133	12/49	$\chi^2 = 2.7$*
Kenya	46/67	10/35	$\chi^2 = 14.9$***
Comparison of localities	$\chi^2 = 17.2$***	$\chi^2 = 0.18$ ns	

* $P < 0.1$; ** $P < 0.05$; *** $P < 0.005$
ns = no significant difference

which is similar to the pregnancy rates of 24 % and 29 % observed during the dry seasons in western Uganda and central Kenya (Table 3).

The sexual activity of adult males was assessed by changes in testes weights. There appeared to be no significant seasonal variation in central Kenya (Fig. 2 A) although larger samples are required to be certain. The sample of adult males from the Crater Track area was also too small to determine seasonal changes. However, there was a significant seasonal variation at Mweya Peninsula (Fig. 1 A). The adult testes attained a mean weight of 1.6 g during the wet periods and regressed to a mean weight of 1.4 g during the dry seasons. The difference in weight was highly significant ($t_{116} = 4.08$, P<0.001). The testes of adult males were also found to regress during the dry season in western Kenya (TAYLOR and GREEN 1976).

Litter size

The variation in litter size in the three main study areas is presented in Table 4. The mean number of implanted embryos was significantly different in the three areas, and the mean number of live embryos was also higher in central Kenya compared to western Uganda. However, the mean number of live embryos was not significantly different in the two localities in western Uganda because of the heavier prenatal mortality at Mweya Peninsula. Other records of litter size include a mean number of embryos of 6.0 (range 2–12) in western Kenya (TAYLOR and GREEN 1976), 4.88 ± 0.54 in Ethiopia (MÜLLER 1977), 2–10 embryos per litter in the northern Sudan (HAPPOLD 1966), and 3–5 embryos per litter in northern Tanzania (MISONNE and VERSCHUREN 1966). The number of young recorded at birth in various laboratory studies include a mean of 5.3 (range 1–11) in a population from Entebbe, Uganda (DAVIS 1963), 4.64 (range 2–7) in a cross between populations from Senegal and Ethiopia (PETTER et al. 1969), and 5–10 young per litter in a population from Senegal (QUILICI et al. 1969). Thus, litter size varies from approximately 3 to 6 depending on the locality.

Litter size appeared to be at a maximum towards the end of the rainy seasons and at a minimum during the dry seasons at Mweya Peninsula (Table 4), and there was also a general trend of increased litter size with increase in maternal body weight. However, these trends were not significant when tested by two-way analysis of variance. The trends should

Table 4

**Monthly variation in mean number of implanted embryos at three localities
in Uganda and Kenya**

Month	Mweya n	Peninsula $\bar{x}$	Crater n	Track $\bar{x}$	Rojewero n	Plains $\bar{x}$
Jan.	2	4.0	–	–	7	5.6
Feb.	2	2.5[1]	–	–	5	5.8
Mar.	2	4.0	2	3.0	–	–
Apr.	9	4.9	1	2.0	1	4.0
May	6	5.7	2	4.5	11	4.2
June	1	4.0	2	4.5	8	7.6
July	4	4.5	1	4.0	–	–
Aug.	2	3.5	–	–	5	4.6
Sept.	5	4.2	1	3.0	–	–
Oct.	9	4.2	2	4.0	–	–
Nov.	1	5.0	3	4.0	9	5.6
Dec.	3	5.7	1	2.0	7	6.1
Mean no.	46[1]	4.54 ± 0.21	15	3.67 ± 0.23	53	5.57 ± 0.24
Implanted S. E.	45[2]	4.62 ± 0.20				
Range	1–10[1]	3–10[2]		2–5		2–12
Mean no live	46[1]	3.93 ± 0.29	15	3.60 ± 0.27	53	5.38 ± 0.23
Embryos S. E.	45[2]	4.0 ± 0.28				
Percent embryos resorbing	13.5[1]	13.5[2]		3.4		1.8

[1] including ectopic pregnancy. – [2] excluding ectopic pregnancy

not be dismissed, however, because the monthly sample sizes were small. An overall comparison of litter size in wet and dry seasons revealed a significant difference at the 10 % level for both implanted embryos ($F_{1,44} = 3.52$; P<0.1) and live embryos ($F_{1,40} = 3.74$; P<0.1). There was no relationship observed between litter size and maternal body weight on the Rojewero Plains, but there was a significant seasonal variation. However, the trend in litter size was not the same in the two breeding seasons (Table 4). In April and May 1975 the litter size was particularly low before peaking at the beginning of the dry season, but in the November 1974 to February 1975 breeding season the litter size was uniformly high. The difference is inexplicable.

Production rates

The potential annual production of young per female in each locality is compared in Table 5. The Kenyan population had approximately twice the potential of the Ugandan populations mainly because of the significantly higher breeding rate. The two Ugandan populations had about the same potential production rates, which was expected because neither their breeding rates or their mean number of live embryos were significantly different. DAVIS (1963) recorded the model interval between births as 21 d and a litter size of 5.3 for a laboratory population from Uganda, which would give approximately the same potential rate of production as found on the Rojewero Plains during the rains. I have estimated the potential production per female from the data presented by TAYLOR and GREEN (1976) and MÜLLER (1977) at 40–50 young per year in western Kenya, and 23 young per year in Ethiopia.

The actual production of young per female was less than the potential because of adult female mortality. A female had the potential of bearing 7 to 12 litters a year in western Uganda and central Kenya. However, counts of placental scars and the presence of

Table 5

Potential mean annual production of young per female at three localities in East Africa

(see Materials and methods)

Locality	Season	Mean interval between litters I (days)	Time period T (days)	Mean number live embryos L	Production of young per female. P	
Rojewero	wet	20.4	166	5.5	45	} 65
Plains	dry	49	199	5.0	20	
Mweya	wet	42.4	244	4.5	26	} 32
Peninsula	dry	68.4	121	3.4	6	
Crater	wet	30	244	3.6	29	} 35
Track	dry	70	121	3.6	6	

embryos indicated that approximately 60 percent of the females in the last six age classes had two or three litters, and the largest number of litters recorded was five for a single female at Mweya Peninsula. This method undoubtedly underestimated the number of litters produced, because as the number of placental scars increased they became increasingly difficult to count accurately, and consequently were not included in the sample. However, it seems unlikely that most females produced more than three or four litters, i.e. one-half to one-third of their potential annual production, and so the observed pregnancy rates must have been achieved by having a high turnover rate of adult females.

Age structure and population dynamics

The monthly age composition of the Mweya Peninsula and Rojewero Plains (Meru) populations indicated a marked seasonal recruitment of young (Fig. 3). Recruitment of age class I individuals mainly occurred during the dry seasons and was generally consistent with the breeding data for the Kenyan population, but was more restricted in time than expected from the breeding data of the Mweya Peninsula population. The much reduced or lack of recruitment at Mweya, during the periods March to April and September to October, suggests an increased mortality of young born at the end of the dry seasons and beginning of the rains. In the Crater Track region the youngest animals were only caught during the periods May to August and November to January, which suggests that recruitment followed a similar seasonal pattern to that observed at Mweya Peninsula.

Both sexes appeared capable of breeding at an early age, particularly during the rains (Fig. 3, Table 6). The central Kenya population appeared to mature at an earlier age than the Ugandan populations (Table 6), which seems reasonable in view of the difference in weight at puberty (Table 1). The delay in maturation of males at Mweya Peninsula

Table 6

Percentage of immature animals and percentage of pregnant or parous females and males with maximum sperm ratings (% adult) in the first five age classes at three localities in East Africa

Age Class	% immature Rojewero	Mweya	Crater	% adult Rojewero	Mweya	Crater
I	71	93	100	10	0	0
II	50	78	100	24	13	0
III	24	52	100	57	33	0
IV	3	22	17	88	68	72
V	0	0	0	97	92	92

compared to the Rojewero Plains is clearly illustrated during the period May to August (Figs. 1 A, 2 A). *Arvicanthis* has also been found to breed at an early age in western Kenya (TAYLOR and GREEN 1976) and in a laboratory population from Senegal (QUILICI et al. 1969), but MÜLLER (1977) found that sexual maturity was late in a population in Ethiopia.

Only a few of the May to July cohort of animals appeared to be present a year later (Fig. 3). This suggests that few animals lived for at least a year and there was a rapid turnover rate. A rapid turnover was also indicated by the study of production rates. All

Fig. 3. Monthly age structure of *Arvicanthis* at two localities. Open blocks represent immature animals and solid blocks represent mature animals

study populations had extremely high potential rates of increase (Table 5) but the trap-per-unit-effort index of population size showed no obvious trends and indicated similar population levels throughout the studies. However, MÜLLER (1977) found that the mortality rate of animals one month old or older was low, and there was a slow turnover of the population in Ethiopia.
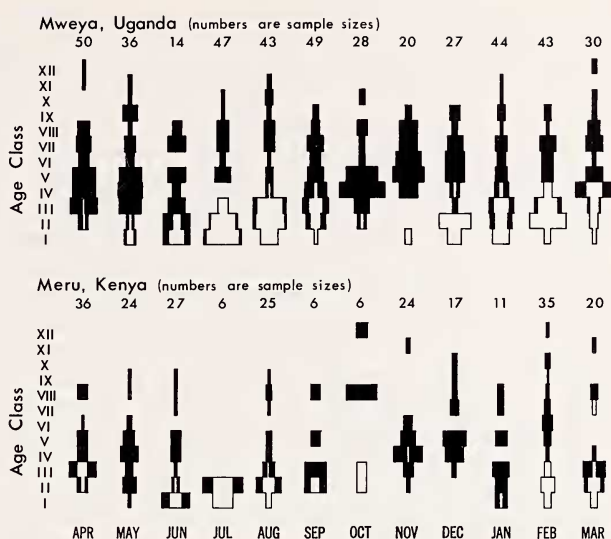
Diet

The analysis of stomach contents of animals caught in central Kenya showed that they ate a wide range of food. They were primarily herbivorous, but also commonly ate insects (Table 7). There was no obvious seasonal trend in the proportion of plant material in the stomachs, but seeds were mainly consumed during the months at the beginning of the dry seasons. The plant material consumed was mainly grass, and dicotyledons were also frequently eaten during the rains and early dry season. There was also a significant amount of unidentified plant material which may have been fragments of stems or tubers. Insects were commonly eaten, comprising nearly one third of the food, and formed the bulk of the stomach contents in 28 % of the animals.

Insects formed a much larger part of the diet compared to that noted in other areas by DELANY (1964), NANDWA (1973), and TAYLOR and GREEN (1976). Otherwise the diet was similar to that found elsewhere, except that cereal crops are a major food item in agricultural areas.

Discussion

Breeding season and environment

Reproductive activity in tropical rodents has conventionally been related to rainfall (DELANY 1972; DELANY and HAPPOLD 1979), because in this region rain is probably the most important factor accounting for seasonal variations in primary productivity. Prop-

osed explanations for this reproductive response to rainfall include 1. increased dietary water intake (BEATLY 1969 and 1976; CHRISTIAN 1979a, b); 2. the stimulative effects of substances found in germinating vegetation (NEGUS and PINTER 1966; REICHMAN et al. 1975; NEGUS and BERGER 1977); and 3. nutritional quality and quantity of available food (FIELD 1975; DELANY and HAPPOLD 1979).

The last two explanations have already been suggested to explain the breeding rhythm of *Arvicanthis*. KINGDON (1974) suggested that green food might provide a biochemical trigger to seasonal breeding in the wild, because WEINBREN and MASON (1957) were able to induce breeding in a laboratory population by adding greenstuffs to their diet; and TAYLOR and GREEN (1976) suggested a relationship between a protein-or carbohydrate-rich diet and reproduction, because in western Kenya breeding mainly occurred when seeds and/or cereals formed the major part of the diet, and the breeding season was extended if wheat was artificially supplied. However, the relationship between breeding and rainfall has been found to be extremely variable in different areas (see Results) and so it seems unlikely that there is a simple single explanation for the reproductive response to rainfall.

Reproduction was continuous in western Uganda (Fig. 1), although in the same area many other rodent species had restricted breeding periods (DELANY and NEAL 1970; NEAL 1977a, b). It would seem, therefore, that *Arvicanthis* is physiologically and ecologically well adapted for continuous breeding. Perhaps a better way of understanding the breeding rhythm of *Arvicanthis* is not to ask what initiates breeding, but rather what prevents the population from breeding continuously?

Breeding ceased towards the end of the dry seasons in central Kenya (Fig. 2), but the cessation of breeding did not seem to be related to the length of the dry period. For example, in August 1974, three months after the previous rains had ended in mid-May, more than half of the adult females collected were pregnant, whereas after a similar length of dry period in March 1975 no pregnancies were observed. The difference in breeding rates seemed to be associated with temperature, with breeding being inhibited by increased temperatures at the end of each dry season. This suggests that animals experienced increased heat or, more likely, water stress which prevented them from breeding during the hottest periods of the year, and would explain the very rapid resumption of breeding once the rains began.

In an afro-alpine area of Ethiopia the situation was almost the opposite, with breeding largely confined to the dry season (MÜLLER 1977). Müller argued that the food supply was sufficient for reproduction throughout the year, which is generally supported by other observations on the climate and vegetation in the same general area (DUNBAR 1978), and that the cessation of breeding during the rains was due to the intolerance of *Arvicanthis* to the cold, moist conditions. DUNBAR (1980) has proposed a similar explanation to account for the negative correlation between births and rainfall in Gelada baboons. The intolerance of cold, moist conditions is presumably species specific because other rodent species only reproduced during the rains and early dry season (MÜLLER 1977).

The cessation of breeding in agricultural areas of western Kenya is more difficult to explain because the seasonal changes induced by the climate were augmented by agricultural activities (TAYLOR and GREEN 1976). The observed relationship between diet and reproduction, namely breeding when seeds and/or cereals formed the major part of the diet and no breeding when the diet switched to vegetative plant tissue, probably did not indicate a simple cause and effect relationship for three reasons. Firstly, breeding rapidly declined or ceased slightly before nutritious food became scarce "allowing resources from the last of the season's weed seeds and cereals to be diverted from reproduction to fat" (TAYLOR and GREEN 1976). Secondly, during the second year of their study, reproduction began before seeds or cereals were detected in the diet. Thirdly, no relationship was observed between diet and reproduction in central Kenya (see Results) and breeding began a few days after the onset of the rains and long before seeds were available. To further

Table 7

Results of analysis of stomach contents of 164 animals collected from the Rojewero Plains

% plant material in stomach	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total n	Total %
>90	1	4	3	–	9	1	2	1	1	14	5	12	53	32
80–89	–	1	2	–	–	2	–	5	–	5	1	6	22	13
70–79	1	–	–	–	3	3	–	2	–	1	1	3	13	8
60–69	1	1	1	1	1	3	–	–	2	5	2	2	19	12
50–59	1	–	–	1	–	–	2	1	1	2	2	1	10	6
40–49	–	2	–	1	2	1	1	1	1	1	1	1	12	7
30–39	–	1	–	1	–	2	2	1	–	1	1	1	10	6
20–29	–	2	–	–	2	–	–	2	2	–	–	–	10	6
10–19	1	1	–	–	–	–	–	1	–	–	–	–	3	2
<10	1	–	–	–	2	–	–	1	2	3	3	–	12	7
seeds plentiful	x	x	–	–	–	–	x	x	–	–	–	x		

(Column header note: Number of animals observed)

Table 8

Comparison of life-history parameters in five populations of *Arvicanthis*

Character	Mweya Trait	Mweya Value	W. Uganda Crater Trait	W. Uganda Crater Value	Ethiopia (Müller 1977) Trait	Ethiopia (Müller 1977) Value	W. Kenya (Taylor and Green 1976) Trait	W. Kenya (Taylor and Green 1976) Value	Central Kenya Rojewero Trait	Central Kenya Rojewero Value
Body size	Large	3	Intermediate	2	Large	3	Intermediate	2	Small	1
Mean litter size	Intermediate	3	Smallest	4	Intermediate	3	Highest	1	High	2
Reproductive rate	Intermediate	3	Intermediate	3	Low	4	High	2	Highest	1
Potential production or growth rate	Intermediate	3	Intermediate	3	Low	4	High	2	Highest	1
Age 1st reproduction	Old	2	Old	2	Old	2	Young	1	Young	1
Total ranking score		14		14		16		8		6
Environmental variability or stress	Low	3	Low	3	Intermediate	2	High	1	High	1

Characters are crudely ranked on a two to four point scale. Characters given a high value are considered to be less opportunistic (i.e. more K-selected) and characters given a low value are considered more opportunistic (i.e. more r-selected)

understand the relationship between diet and reproduction it is important to follow the seasonal changes in this area. Animals were collected from relatively small areas of uncultivated land separating fields. Towards the end of the rains these areas were surrounded by large areas of cereal crops (mainly maize) which were available for colonization and a source of food. At the end of the rains and beginning the dry season the highly favourable crop habitat was destroyed during the course of a few days by harvesting, and rodents were forced to take refuge in the small uncultivated areas. The cessation of breeding soon after may have been linked to the increased density, due to immigration, relative to the food supply, which would explain why animals stopped breeding before nutritious food became scarce. The density for the remainder of the dry season was probably frequently in excess of the carrying capacity, because TAYLOR and GREEN (1976) mention that the grass cover was reduced by feeding activity. Breeding did not resume until two to three months after the onset of the rains. The delay in reproduction, compared to my observations in central Kenya, may have been due to physiological damage similar to that suggested for a *Microtus* population in California (LIDICKER 1973). The suggestion that the breeding rhythm was a result of a subtle interplay of density and food supply would explain the observed relationship of diet and reproduction, and also why the breeding season could be lengthened by augmenting the food supply.

The various hypotheses to account for the cessation of breeding, and hence the breeding rhythm of *Arvicanthis*, in different localities could be tested by a series of field experiments. The suggestion that increased water stress, due to higher temperatures, inhibited breeding in central Kenya could be tested by a field experiment, similar to that performed by CHRISTIAN (1979b), in which animals were provided with supplementary drinking water in an experimental area. The hypothesis would be supported if breeding was extended in experimental areas compared to control areas. MÜLLER's hypothesis that breeding was inhibited by cold, wet conditions in Ethiopia would be more difficult to test, because if warm sheltered conditions were provided other features of the environment might also be changed. However, if a laboratory population were maintained and fed a normal diet during the rains, breeding should be continuous if cold wet conditions are a key factor. The hypothesis that increased density relative to the food supply inhibited breeding in western Kenya could be tested by reducing and maintaining a low density of small rodents from the middle of the rains until the following rains. The breeding season should be extended if density is an important factor.

Life history strategy

The various populations of *Arvicanthis* differed in life history characteristics such as body size, mean litter size, reproductive rates etc. (see results) and so it is of interest to see how the data relate to current ideas about life history tactics (see STEARNS 1976, 1977; SOUTHWOOD 1976; HORN 1978).

Life history characteristics were crudely ranked on a two to four point scale (Table 8) with the highest values being assigned to those considered to be more K-selected, and the lowest values to those considered to be more r-selected. I recognize the crudeness and limitations of this classification, but similar classifications by TAMARIN (1978) and CRISTIAN (1979) have helped our understanding of the adaptive significance of differences in life history characteristics between species. It has been suggested that it may be difficult to compare strategies of different populations or species when there are seasonal changes in strategy (NICHOLS et al. 1976). However, seasonal changes in litter size and reproductive rates posed few problems when they were ranked, because the differences were large and the seasonal changes, where known, were similar. The amplitude of the seasonal changes did vary, and this aspect of life history strategy warrants further investigation. The ranking of environmental variability, or stress, was difficult and rather subjective. The environment

was considered to be most variable in the two localities in Kenya. In central Kenya the rainy periods were of short duration (approximately 3 months each year) and the long dry periods were hot; and in western Kenya, although the rains were of long duration (approximately 8 months), the food supply and population distribution were severely disrupted by agriculture. The environment was considered to be of intermediate variability in Ethiopia, because although the rains were relatively short (3 to 4 months), there were ground frosts throughout the year (DUNBAR 1978) and so the dry season was not as extreme as that at lower altitudes. The least variable environment in terms of climate was clearly in western Uganda, but there was also a probability of fire in both study areas (DELANY 1964; NEAL 1970) so that it may have been more stressful than indicated.

There was a fairly high correlation between the relative ranks of the various life history parameters (Table 8), and the results were generally in accord with conventional ideas on r- and K-selection. In particular, the trend in body size supports the theory of r- and K-selection, rather than the suggestion of BOYCE (1979) that body size increases in more seasonal environments. The different populations could be divided into two main groups. Those in western Uganda and Ethiopia were relatively more K-selected than the Kenyan populations and were associated with less variable environments (Table 8). Thus, as the environment becomes more stressful, *Arvicanthis* responds by diverting more energy into production with a corresponding decrease in average life span and increase in turnover rate.

Acknowledgements

Zusammenfassung

Die Fortpflanzungsbiologie der Kusu-Grasratte, Arvicanthis, in Ostafrika

In zwei Gebieten in West-Uganda und einem in Zentral-Kenia wurden über das ganze Jahr verteilt insgesamt 749 *Arvicanthis* gesammelt, um ihre Fortpflanzungsbiologie unter verschiedenen Umweltbedingungen zu vergleichen.

In West-Uganda pflanzten sich die Grasratten zu allen Jahreszeiten fort, doch war die Vermehrungsrate hier während der Regenzeit höher als während der Trockenperioden. In Zentral-Kenia setzte die Fortpflanzungstätigkeit gegen Ende der Trockenzeit, als die Temperatur am höchsten war, ganz aus und begann erneut einige Tage nach dem Einsetzen der Regenzeit. Zwischen der Art der aufgenommenen Nahrung (nach Analysen von Mageninhalten) und der Fortpflanzungsintensität wurde kein Zusammenhang gefunden. Vielleicht wird die Fortpflanzung durch steigenden Wassermangel gehemmt. Daß dies nicht überall so ist, zeigen die unterschiedlichen Beziehungen zwischen Niederschlägen und Fortpflanzungszeiten in verschiedenen Regionen Afrikas.

Beim Vergleich von fünf Untersuchungsgebieten zeigte sich: Je veränderlicher die Umweltbedingungen sind, um so höher sind die Wurfstärken und Fortpflanzungsraten und um so geringer das Alter bei Erreichen der Geschlechtsreife und die Körpergröße. Dies steht in Einklang mit der Theorie der r- und K-Selektion.

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Subspecies and clines in the Springbok *(Antidorcas)*

Notes on Gazelles, 2

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Abstract

Studied the nature of geographic variation in the Springbok. There is only one species, *Antidorcas marsupialis* Zimmermann, 1780, but three subspecies can be sharply demarcated, despite the presence of wellmarked clines within at least two of them.

Introduction

Though not generally classed under the heading of "gazelle", the Springbok ist clearly one of a cluster of antelopes springing from that general stock. It seems probable that the currently accepted classification simply separates out a few distinctive types as genera – *Antidorcas, Procapra, Litocranius,* perhaps even *Antilope* – while the mass of more